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Response of Diptera populations to experimentally modified leaf litter input in a beech forest on limestone

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With 7 figures

1. Introduction

In forest ecosystems, the formation of humus types depends on a variety of factors (soil parent material, abiotic soil factors, climate, tree species). On the other hand, the composition of soil biota is related to humus type: mull soils are characterized by high zoomass and high macrofauna abundance, whereas in moder soils zoomass is lower and mesofauna abundance is high (SCHAEFER & SCHAUERMANN, 1990). As litter layers are rather thin in mull soils but well-developed in moder soils, it may be hypothesized that the composition of the decomposer community may be to some degree dependent on the amount of litter present on the forest floor.

Litter provides nutrients and energy for the decomposer community. Therefore, additional litter input may result in an increase of decomposer populations, whereas reduced input rates should cause a decline in abundance due to starvation. However, quantitative variation in litter input may also cause changes in other properties of the litter layer (e.g. water retention capacity, structural features), which by favouring some taxa and hampering others could modify decomposer community structure. Thus, additional litter input to mull soils may result in litter layer conditions supporting a decomposer community that rather resembles one typical for moder soils.

The present paper reports on the response of dipterous populations to experimental modifications of herbaceous and canopy leaf litter input in a mull soil beech forest, where canopy leaf litter (62,6%) and herbaceous leaf litter (18,8%) account for the major part of annual above ground litter input (SCHAEFER, 1990). Further, the results are analyzed in order to evaluate the influence of macroclimate, microclimate and food accessibility on the numerical responses of Diptera in this perturbation experiment.

Some results concerning larval populations of Diptera have been published previously (HÖVEMEYER, 1987, 1989). In this paper, however, data are presented on adult Diptera captured after emergence. Thus, information on the response of particular species became feasible.

2. Materials and methods

The study site was situated in a submontane beech forest on limestone (Melico-Fagetum; rd. 420 m a.s.l.) near Göttingen, FRG. Further details are given by SCHAEFER & SCHAUERMANN (1990; "Göttinger Wald") and references therein. Experiments were conducted in an area where *Allium ursinum* L. and *Anemone nemorosa* L. were the dominant spring geophytes.

Four types of experimental plots (10 by 10 m each) were established:

0L (canopy leaf litter exclusion): on four plots autumnal leaf litter fall was excluded every year (1981—1987);

3*

1L (control plots): eight plots with undisturbed litter conditions were selected as controls;

5L (litter multiplication): on two plots the autumnal canopy litter input was raised to five times the natural amount both in November 1981 and 1982;

OH (herbaceous leaf litter exclusion): from one plot all herbaceous plants and seedlings of trees were removed for three years starting in spring 1982.

In order to catch adult Diptera emerged from the soil, four emergence traps (FUNKE, 1971) per treatment, each covering 1 m² of ground were set up in 1983. As most dipterous larvae are not very mobile organisms, they are not likely to invade the experimental plots by themselves. Instead, spatial distribution is largely determined by females selecting oviposition sites favourable to larval development. Thus, sampling did not start before 1983, allowing for females making their choice in the course of 1982 (i.e. after the first removal and multiplication of litter input). From 1984 until 1987 five emergence traps per treatment, each covering 1/4 m² of ground, were used. No catches were made on the OH-plot in 1986 and 1987 and, in 1987, four large (1 m²) emergence traps were installed on the OL-plots. Emergence traps were set up in March each year and were not moved until mid-December. Catches were mostly collected at biweekly intervals.

Imagines were identified to species except Chironomidae, Cecidomyiidae, Phoridae and a few acalyptrate families of minor importance.

Catches of adult Diptera were subdivided into eleven trophic groups according to the feeding habits of their respective larvae (HÖVEMEYER, 1984, 1991). Some of these should be defined briefly. Three types of predatory larvae were distinguished: aphidophagous feeders, parasitoids and "other zoophagous feeders". The last-named group comprises taxa with soil-dwelling larvae which prey on other soil animals. Four trophic groups of larvae are more or less directly involved in the decomposition process: phytosaprophagous, microhumiphagous, mycetophagous feeders and "surface scrapers". The term "phytosaprophagous" is restricted to larvae directly feeding on leaf litter. In the microhumiphagous feeders mainly algae, Testacea, fungal and amorphous humic material are consumed. The majority of mycetophagous feeders (i.e. most soil-dwelling cecidomyiid larvae) supposedly suck the fluid contents from fungal hyphae (HEALEY & RUSSELL-SMITH, 1971). The "surface scrapers" seem to live
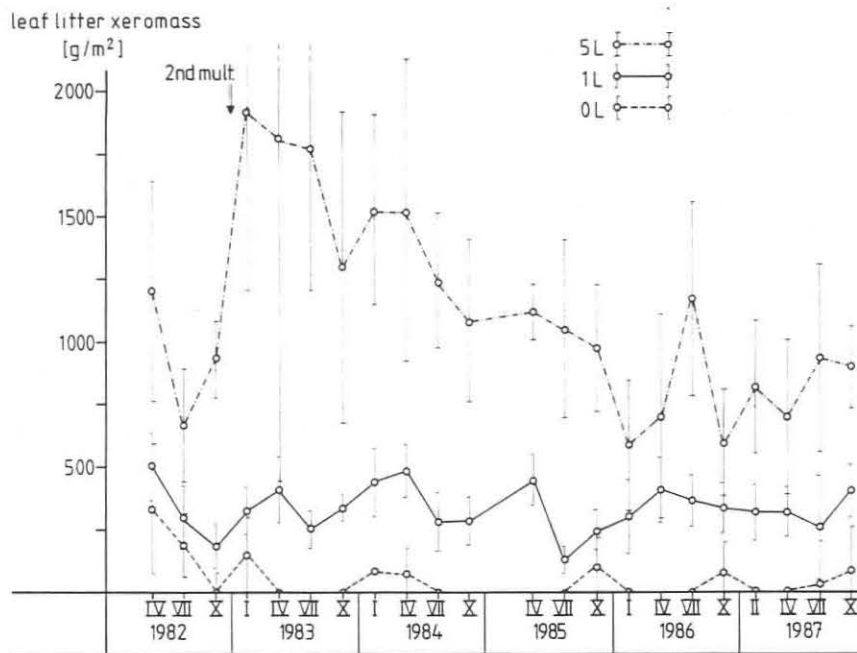

Fig. 1. Standing crop of leaf litter xeromass in the litter layers on experimental plots with modified autumnal canopy leaf litter input in a beech forest on limestone (1982—1987). 5L = leaf litter multiplication, 1L = control, OL = leaf litter exclusion, 2nd mult. = date of second multiplication, standard deviations (for n = 6 in most cases) are indicated.

on diets similar to microhumiphagous feeders, although a different feeding technique has been adopted (HEALEY & RUSSEL-SMITH, 1971).

"Production of imagines" (FUNKE, 1971) was estimated after assignation of trapped Diptera adults to twelve size-classes with fixed xeromass values progressing geometrically (HÖVEMEYER, 1985, 1991).

Xeromass of canopy leaf litter in the litter layer was calculated as described by HÖVEMEYER (1989).

During the study period, weather varied considerably from year to year. Compared to long-term means, moisture regimes in early/mid summer were as follows: 1982: dry/dry, 1983: normal/dry, 1984: wet/normal, 1985: wet/normal, 1986: normal/normal, and 1987: wet/normal. Some graphs are provided by HÖVEMEYER (1991).
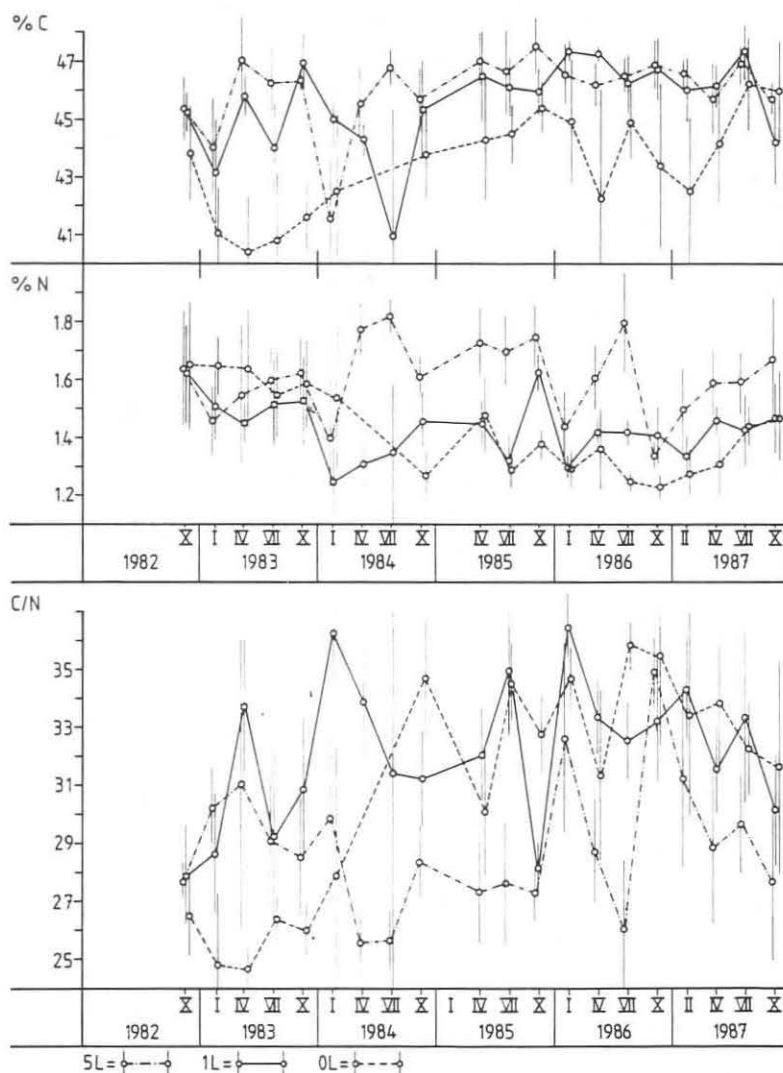

Fig. 2. Mean carbon (%C) and nitrogen (%N) contents and C/N ratios of leaf litter in the litter layers on experimental plots with modified autumnal canopy leaf litter input in a beech forest on limestone (1982–1987). See fig. 1 for abbreviations; standard deviations (for n = 6 in most cases) are indicated.

3. Results and discussion

3.1. General properties of experimental plots

After the second multiplication, a decline of leaf litter xeromass was observed on the 5L-plots. However, values did not level out with the controls at the end of the study period (fig. 1). On the OL-plots canopy leaf litter was decomposed rather quickly and after two years of exclusion the litter layer was made up almost completely of fine woody material. Values for the OH-plot were very similar to controls and were omitted from fig. 1 for clarity.

Carbon content in the litter layer was generally lower on the OL-plots compared to the 5L- and 1L-plots but nitrogen content tended to be rather high during the first two study years as freshly fallen leaves were lacking after exclusion (fig. 2). On the 5L-plots nitrogen content was similar to control values during the first two years, but increased in 1984 and 1985.

C/N-ratios can be taken as a rough measure of food quality. It was found that values for the OL-plots were lower than controls in 1983, but during the later study years a new equilibrium, almost exclusively based on the input of woody material and herbaceous leaf litter, had established itself at a level similar to controls. In 1983 there were no big differences between 5L- and 1L-plots, but in 1984 and 1985 C/N-ratios were distinctly lower on the multiplication plots compared to controls.

Naturally, the thick litter layers on the 5L-plots had a high water retention capacity and remained moist — at least in the deeper strata — even in the hot dry summers of 1982 and 1983 (HÖVEMEYER, 1985). As Diptera larvae are quite sensitive to desiccation they were thus offered a favourable and rather stable environment on the 5L-plots. However, soil moisture content was very similar under all experimental conditions (HÖVEMEYER, 1985). As to the OL-plots, this can be attributed to mosses which had colonized the forest floor after leaf litter had vanished. Compared to controls, yearly and daily fluctuations of soil temperature were dampened after leaf litter multiplication but more distinct after leaf litter exclusion.

3.2. Responses of Diptera

3.2.1. Family and species numbers

During the entire study 38 Diptera families were recorded from the catches and 217 species were identified[1]. Total family numbers were rather similar for all treatments, but the 5L-plots yielded more families per annual catch. Similar results were obtained for species numbers (table 1).

Table 1. Family and species numbers of adult Diptera captured in emergence traps on experimental plots with and without manipulated leaf litter input in a beech forest on limestone (1983–1987).

treatment number of study years	1L 5	5L 5	0L 5	0H 3	total
total number of families	32	34	31	30	38
mean number of families per annual catch	24.0	26.4	21.6	22.6	
total number of species	124	164	118	86	217
mean number of species per annual catch *	52.0	67.6	41.4	40.0	

Note: 1L = control, 5L = canopy leaf litter multiplication, 0L = canopy leaf litter exclusion, 0H = herb leaf litter exclusion. * corrected for differences in ground area sampled in different study years.

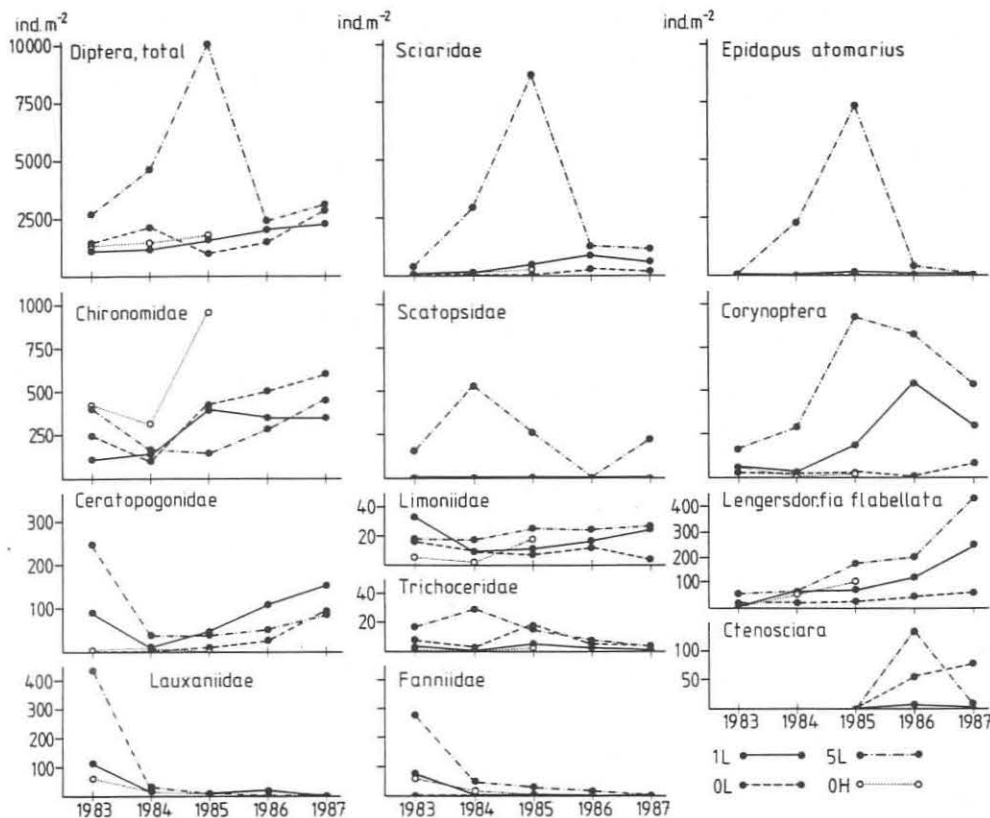[1] A complete list is available on request.

Fig. 3. Annual emergence abundances (ind./m²) of total Diptera and selected taxa on experimental plots with modified leaf litter inputs in a beech forest on limestone (1983–1987). All genera and species shown in the right hand column belong to the family Sciaridae. OH = herb leaf litter exclusion; for further abbreviations see fig. 1.

3.2.2. Emergence abundance

Annual emergence abundances of various dipterous taxa are shown in fig. 3 and incidents of significant differences (U-test) between controls and other treatments are listed in table 2. The main results are as follows:

1. Annual emergence abundances of total Diptera were highest on the 5L-plots in each of the five study years (fig. 3).

2. Peak values on the 5L-plots in 1984 and 1985 were largely due to mass developments of the sciarid species *Epidapus atomarius* (DEGEER, 1778) in 1984 and 1985 (fig. 3, upper row).

3. In many families, emergence abundance increased after leaf litter multiplication (fig. 3). Sciarid and fanniid numbers were significantly higher on the 5L-plots relative to controls in four out of five study years (table 2). Emergence abundance of the sciarid genus *Corynoptera* was 1.5 to 7.6 times as high as control values.

4. Herb litter exclusion resulted in an increase of chironomid emergence abundance (fig. 3, table 2). As chironomid larvae are often encountered mining dead rootlets in the soil, this may be due to an increase in the standing crop of below-ground herb litter following removal of the above-ground plant parts.

5. As expected, leaf litter exclusion resulted in a decrease of emergence abundance in most dipterous taxa (fig. 3). Ceratopogonidae and — following the disappearance of leaf

Table 2. Significant differences (U-test, $p < 0.05$) of emergence abundances of adult Diptera between sampling plots with experimentally modified litter layers and controls in a beech forest on limestone.

treatment study year	5L '83	5L '84	5L '85	5L '86	5L '87	0L '83	0L '84	0L '85	0L '86	0L '87	0H '83	0H '84	0H '85
Ceratopogonidae						−	−	−	−				−
Chironomidae			−								+	+	+
Bibionidae			+										
Sciaridae	+	+	+		+		−	−	−				
Scatopsidae		+	+										
Lestremiinae								−		−			−
non-lestremiine Cecidomyiidae							+		+	+	+		
Syrphidae					+				+	−	−		−
Lauxaniidae	+			−		−	−	−	−	−	−		
Sciomyzidae										−			
Fanniidae	+	+	+		+	−	−						
Muscidae	+				+	−							

Note: $+/-$ = higher/lower relative to controls; OH = herb leaf litter exclusion; See tab. 1 for further abbreviations.

litter — Sciaridae were significantly reduced on the 0L-plots (table 2). Canopy leaf litter exclusion also resulted in a complete breakdown of lauxaniid and fanniid populations (fig. 3, table 2). During the last three study years, no more than 15 lauxaniid and two fanniid adults were captured on these plots! On the other hand, non-lestremiine Cecidomyiidae performed very well after canopy leaf litter exclusion. In this group, the gall-making Cecidomyiidae are predominant. Their larvae enter the soil for aestivation and/or hibernation after pupation. Thus, high emergence abundance in this group should possibly be attributed to reduced predator abundance (e.g. spiders, STIPPICH, 1986) on the 0L-plots.

3.2.3. Trophic groups of larvae

As exemplified in the non-lestremiine Cecidomyiidae, it is essential to take into account larval feeding habits in order to achieve a better understanding of the responses to litter manipulations exhibited by particular dipterous groups. Annual emergence abundances of adult Diptera divided into trophic groups of larval feeding habits are presented in table 3. A distinction should be made between groups with larvae entering the soil merely for pupation/pupariation, aestivation and/or hibernation (e.g. aphidophagous, phytophagous feeders) and those with larvae living in particular minor habitats (e.g. xylophagous and necrophagous feeders) on the one hand, and groups with larvae actually developing in the soil or litter layer (e.g. phytosaprophagous feeders, surface scrapers), on the other.

The first two groups exhibited few distinct differences between experimental treatments and controls. Presumably, due to a reduction of food resources (dead earthworms, snails, slugs, and soil arthropods) the number of necrophagous feeders declined on the 0L-plots after the litter layer had disappeared, whereas comparatively high numbers were maintained on the 5L-plots. Coprophagous feeders were found in rather high numbers on the multiplication plots in 1984 and 1985 where mice runs appeared to be particularly numerous.

Emergence abundance of Diptera with soil dwelling larvae (marked by bold letters in tables 3. and 4.) was highest on the multiplication plots and lowest on the exclusion plots in each of the study years. The same is true for the phytosaprophagous feeders (with one single exception in 1983: $OL > OH$). This trophic group is largely identical with the Sciaridae. Similar patterns were obtained for the surface scrapers, which correspond to the families Lonchopteridae, Lauxaniidae, and Fanniidae. Mycetophagous feeders were more

abundant on the 5L-plots compared to controls. However, on the OL-plots they seem to have been initially favoured when the litter layer was diminishing, whereas complete absence of leaf litter had been unfavourable.

In the microhumiphagous feeders (mainly Chironomidae and Ceratopogonidae) an increase was observed on the 5L-plots in 1983 followed by a decline in numbers. In 1987, however, the population had recovered again. On the OL-plots, an initial decline of abundance was followed by an increase above control levels. Whereas larval populations of Chironomidae had been dominated by *Paraphaenocladius* larvae, which are known to migrate from the soil into the litter layer in early winter, genera with constantly soil-dwelling larvae were dominant on the OL-plots from 1984 on (HÖVEMEYER, 1985).

Annual emergence abundance values of Diptera with predatory larvae were similar on all experimental plots and no pattern became evident in these species.

3.2.4. Production of imagines

Data on the 'production of imagines' (FUNKE, 1971) are presented in Table 4. Overall patterns are similar to abundance data, but production of Diptera with phytosaprophagous larvae was much higher on the canopy leaf litter exclusion plots than could have been expected. This is due to the fact that the proportion of larger species mainly from the families Tipulidae, Trichoceridae and Bibionidae had increased on these plots. Some species from these families were found to be associated with moss cushions. On the OH-plots production of phytophagous species was very low, as the large species feeding on herbs (i.e. *Cheilosia fasciata* SCHINER et EGGER, 1853, *Portevinia maculata* (FALLÉN, 1817) (Syrphidae), some Scatophagidae and Anthomyiidae) had been excluded. Thus the remaining figures represent taxa with phytophagous larvae developing in the canopy layer (i.e. Cecidomyiidae).

3.2.5. The dipterous decomposer community

In terms of biomass, the significance of decomposers is considerably lessened compared to dominance values (tables 3 and 4) as most decomposer species are rather small. Nevertheless, taxa with larvae directly involved in the decomposition process might be expected to show the most striking responses to litter input manipulation. That is why the following considerations will be restricted to the microhumihages, mycetophages, phytosaprophages and the surface scrapers, i.e. the 'dipterous decomposer community'.

As to the 5L-, 1L- and OH-plots, the first study year (1983) stands out from those following due to a mass development of surface scrapers. As the respective species are rather large, this finding becomes even more obvious when biomass values are considered. On the OL-plots, however, surface scrapers had been excluded due to lack of fresh canopy leaf litter (fig. 4).

On the multiplication plots, phytosaprophagous feeders were the most important group from 1984 on (table 3), with dominance values higher than for any other treatment (fig. 4). Increase of phytosaprophagous feeders was balanced by decreasing proportions of microhumiphagous feeders.

A mean linkage clustering procedure was adopted in order to evaluate degrees of similarity in the dipterous decomposer community as reflected by the annual catches from the experimental plots. (fig. 5). Five distinct clusters are recognized in fig. 5 and each is characterized by the predominance of one particular trophic group (table 5).

Table 3. Annual emergence abundances (ind/m^2) of Diptera adults arranged according to the feeding habits of their respective larvae on experimental plots with modified leaf litter inputs in a beech forest on limestone (1983–87).

treatment study year	1L 1983	1L 1984	1L 1985	1L 1986	1L 1987	5L 1983	5L 1984	5L 1985	5L 1986	5L 1987	OL 1983	OL 1984	OL 1985	OL 1986	OL 1987	OH 1983	OH 1984	OH 1985
larval feeding habits																		
aphidophagous	2	—	—	—	9	4	1	—	—	6	—	—	—	1	1	0	—	—
parasitoids	10	10	—	1	1	7	6	2	1	5	10	5	1	1	4	9	12	5
zoophagous, others	**28**	**16**	**50**	**28**	**46**	**47**	**10**	**25**	**44**	**62**	**20**	**6**	**39**	**30**	**50**	**20**	**11**	**7**
necrophagous	296	151	77	205	76	219	213	250	222	137	292	283	52	65	65	194	212	78
coprophagous	1	—	1	4	2	4	47	38	6	1	2	3	—	1	4	2	—	—
microhumiphagous	**201**	**152**	**429**	**460**	**506**	**644**	**205**	**198**	**341**	**546**	**248**	**102**	**439**	**530**	**706**	**430**	**326**	**963**
surface scrapers	**201**	**39**	**27**	**34**	**14**	**738**	**84**	**52**	**27**	**26**	**11**	**—**	**1**	**4**	**6**	**143**	**30**	**26**
mycetophagous	**42**	**181**	**286**	**277**	**288**	**234**	**299**	**334**	**287**	**502**	**148**	**294**	**194**	**251**	**169**	**81**	**364**	**236**
phytosaprophagous	**160**	**171**	**542**	**933**	**685**	**596**	**3544**	**9029**	**1354**	**1398**	**105**	**91**	**142**	**312**	**270**	**100**	**137**	**430**
xylophagous	1	2	—	—	2	6	2	—	4	—	—	—	—	—	—	—	2	—
phytophagous	161	427	142	82	610	131	214	102	65	470	550	1329	87	262	1579	334	350	107
unknown	—	—	—	2	1	—	—	1	2	1	—	—	2	—	4	—	—	—
total Diptera	1102	1150	1553	2026	2238	2630	4625	10030	2353	3153	1385	2114	958	1456	2857	1312	1444	1851
soil-dwelling larvae	**632**	**560**	**1334**	**1732**	**1538**	**2259**	**4142**	**9638**	**2054**	**2534**	**532**	**494**	**816**	**1126**	**1201**	**773**	**868**	**1662**
% of total Diptera	**57**	**49**	**86**	**86**	**69**	**86**	**90**	**96**	**87**	**80**	**38**	**23**	**85**	**77**	**42**	**59**	**60**	**90**
decomposers	604	544	1283	1704	1492	2212	4132	9613	2010	2472	512	487	777	1097	1150	753	856	1654
% of total Diptera	**55**	**47**	**83**	**84**	**67**	**84**	**89**	**96**	**85**	**78**	**37**	**23**	**81**	**75**	**40**	**57**	**59**	**89**

Note: 1L = controls; 5L = canopy leaf litter multiplication; OL = canopy leaf litter exclusion; OH = herb leaf litter exclusion.

Table 4. Production of Diptera adults (xeromass, mg m_x/m^2) arranged according to feeding habits of their respective larvae on experimental plots (1983—87).

treatment	1L	1L	1L	1L	1L	5L	5L	5L	5L	5L	OL	OL	OL	OL	OL	OH	OH	OH
study year	1983	1984	1985	1986	1987	1983	1984	1985	1986	1987	1983	1984	1985	1986	1987	1983	1984	1985
larval feeding habits																		
aphidophagous	12	—	—	—	54	25	5	—	—	39	—	—	—	2	2	2	—	—
parasitoids	5	7	—	0	0	6	6	10	10	3	9	1	0	2	3	2	7	6
zoophagous	**21**	**18**	**32**	**18**	**48**	**64**	**15**	**22**	**27**	**62**	**13**	**2**	**18**	**10**	**23**	**13**	**25**	**7**
necrophagous	57	30	16	37	14	48	40	39	41	25	56	54	10	12	12	37	41	14
coprophagous	0	—	1	7	2	4	32	16	4	1	8	2	—	5	10	1	—	—
microhumiphagous	**22**	**9**	**33**	**37**	**45**	**63**	**15**	**15**	**24**	**' 39**	**12**	**5**	**22**	**29**	**47**	**21**	**17**	**47**
surface scrapers	**108**	**23**	**18**	**15**	**6**	**391**	**51**	**32**	**17**	**16**	**6**	**—**	**1**	**2**	**2**	**79**	**18**	**12**
mycetophagous	2	9	21	13	17	15	21	40	15	28	8	14	10	13	9	4	19	19
phytosaprophagous	**29**	**17**	**36**	**57**	**57**	**51**	**136**	**280**	**117**	**179**	**25**	**51**	**53**	**56**	**40**	**15**	**11**	**34**
xylophagous	1	1	—	—	1	4	20	—	3	—	—	—	—	—	—	—	2	—
phytophagous	62	72	181	61	131	30	71	17	69	298	103	161	187	193	125	16	19	5
unknown	—	—	—	7	5	—	—	2	12	0	—	—	15	—	35	—	—	—
total Diptera	319	185	336	253	381	700	412	474	338	689	239	291	315	324	308	192	158	144
soil-dwelling larvae	**182**	**76**	**139**	**141**	**173**	**583**	**238**	**389**	**200**	**323**	**64**	**72**	**104**	**109**	**122**	**133**	**89**	**119**
% of total Diptera	**57**	**41**	**41**	**56**	**45**	**83**	**58**	**82**	**59**	**47**	**27**	**25**	**33**	**34**	**40**	**69**	**57**	**83**
decomposers	161	58	107	122	125	519	223	367	172	262	51	70	85	100	99	120	65	112
% of total Diptera	**51**	**31**	**32**	**48**	**33**	**74**	**54**	**77**	**51**	**38**	**21**	**24**	**27**	**31**	**32**	**63**	**41**	**78**

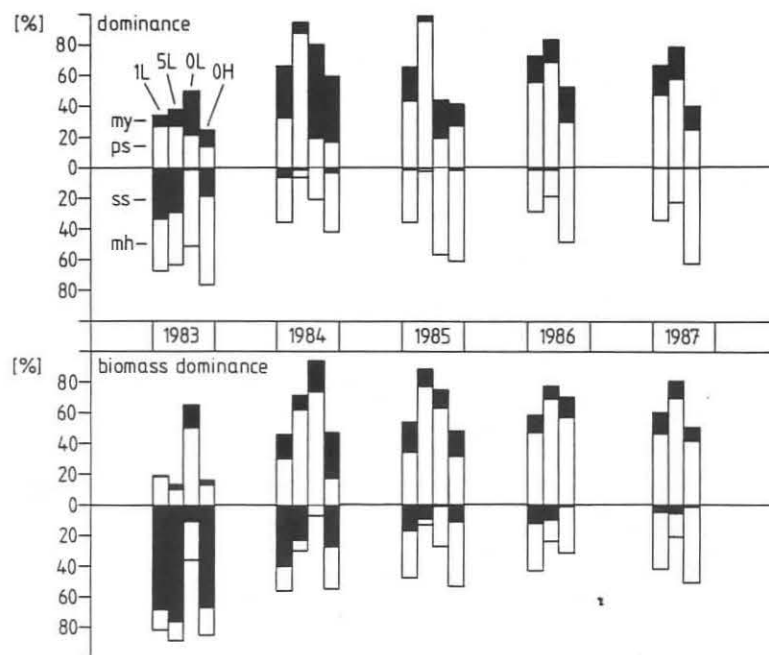Note: See table 3 for abbreviations.

Fig. 4. Dominance and biomass dominance structure in the dipterous decomposer communities on experimental plots with modified leaf litter inputs in a beech forest on limestone as reflected by adults captured in emergence traps (1983–1987). 1L = controls, 5L = canopy leaf litter multiplication, OL = canopy leaf litter exclusion, OH = herb leaf litter exclusion, my = mycetophagous feeders, ps = phytosaprophagous feeders, ss = surface scrapers, mh = microhumiphagous feeders.
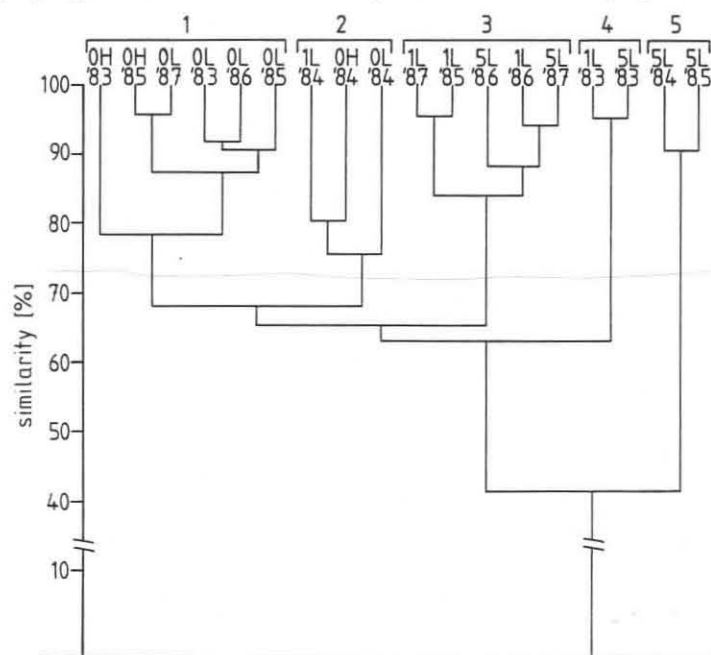

Fig. 5. Trophic group percent similarity relationships in the dipterous decomposer communities of experimental plots with modified leaf litter inputs in a beech forest on limestone (1983–1987). See table 3 for abbreviations; 1 to 5 = cluster numbers referred to in table 5 and the text.

Table 5. Average within-cluster (1−5, fig. 5) dominance values (%) of Diptera with larvae constituting the dipterous decomposer community arranged according to larval feeding habits (standard errors in brackets).

cluster (fig. 5) larval feeding habits	1	2	3	4	5
mycetophagous feeders	19,4 (2,9)	45,3 (7,9)	18,5 (1,4)	8,7 (1,8)	5,4 (1,9)
microhumiphagous feeders	55,0 (2,2)	29,0 (5,0)	26,7 (3,3)	31,2 (2,1)	3,5 (1,5)
surface scrapers	3,9 (3,0)	3,6 (2,1)	1,5 (0,3)	33,4 (0,0)	1,3 (0,8)
phytosaprophagous feeders	21,7 (2,2)	22,1 (4,8)	53,4 (4,4)	26,7 (0,3)	89,9 (4,1)

The first cluster combines the majority of annual catches from exclusion plots (fig. 5) where microhumiphagous feeders were dominant. Mycetophagous feeders were the most important group in cluster 2, which includes the 1984 catches from non-multiplication plots. It seems that lestremiine Cecidomyiidae (the main constitutents of this group) were less affected by the dry summers of 1982 and 1983 than other dipterous taxa. Phytosaprophagous feeders attained the largest proportion in the third cluster (table 5), which includes three annual catches from control plots and the two final ones from 5L-plots. As weather conditions had been fairly normal during the developmental period of larvae in the respective generations and differences between 5L- and control plots had decreased (fig. 1 & 2), it seems reasonable to suggest that cluster 3 represents the normal composition of the dipterous decomposer community in the beech forest considered.

The two remaining pairs were characterized by increased significance of surface scrapers (cluster 4) and extremely high dominance values attained by phytosaprophagous feeders (cluster 5; fig. 5, table 5), respectively.

Similarity relationships of annual catches may also be analysed with respect to species dominance values (fig. 6A). However, it should be noted that only a fraction of the dipterous decomposer community could be considered as some families were not identified to species (cf. chapter 2). The overall pattern is that within-year similarities tended to be higher than within-treatment similarities, i.e., in most cases catches made during one particular study year were more closely related than those obtained from one particular experimental plot during several successive study years. However, there are some exceptions to this rule: in particular, communities obtained from the multiplication plots in 1984 and 1985 showed the highest degree of similarity (fig. 6A). If the clustering procedure is restricted to species with phytosaprophagous larvae (fig. 6B) the result changes but a little. However, the community of phytosaprophages encountered on the multiplication plots in 1983 exhibited a closer relationship to those of 1984 and 1985 (fig. 6B) compared to the overall decomposer communities considered above (fig. 6A). This is due to the fact that the surface scraper families Fanniidae and Lauxaniidae which attained high dominance values in 1983 had been removed from the analysis.

3.3. Causes of Diptera respones

The analysis of data obtained from the litter manipulation experiment is far from easy as Diptera populations are subject to a variety of environmental factors: the most important are macroclimate, moisture (microclimate) and food availability. HÖVEMEYER (1991) has shown that in many families emergence abundance of adults is positively correlated with wet weather conditions during the previous summer, i.e. when larvae are small and particularly sensitive to desiccation. However, there is a hierarchy within the three factors as wet weather condititions will usually result in high moisture content in the soil and in the
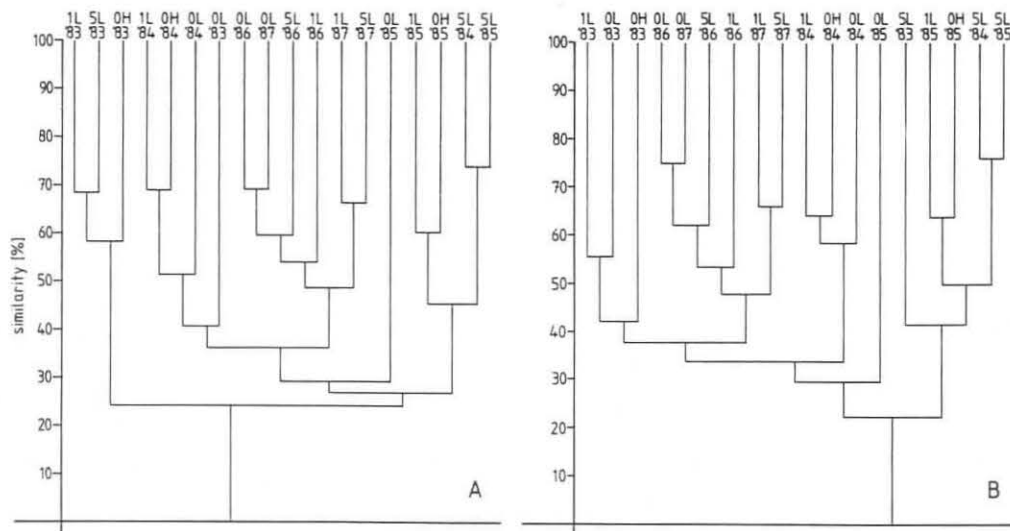
Fig. 6. Species percent similarity relationships in the dipterous decomposer communities (A) and the phytosaprophagous feeder communities (B) of experimental plots with modified leaf litter inputs in a beech forest on limestone (1983–1987). See table 3 for abbreviations.

litter layer. This, in turn, will be favourable to dipterous larvae in two ways: (i) larval mortality due to desiccation will be reduced and (ii) food supply, i.e. food accessibility, will be increased. Thus, no distinction between the significances of macroclimate, microclimate and food accessibility can usually be made based on abundance values alone.

As to the canopy leaf litter exclusion plots, it is impossible to decide whether reduction of Diptera abundance was due to lack of food or unfavourable abiotic conditions. However, some mechanisms causal to Diptera responses to litter input manipulation may be revealed by comparing data from 5L- and control plots. Three alternative hypotheses can be formulated:

1. If macroclimate was the main driving variable determining numbers of Diptera, we should expect abundance curves (fig. 3) to show similar trends for all treatments throughout the study period, although abundance values may be higher for the 5L-plots and lower for the 0L-plots compared to controls due to differences in food supply. Likewise, dipterous decomposer community structure should be rather similar on the 1L- and 5L-plots, at least within years.

2. If moisture content was the main driving variable we should expect emergence abundances to be higher on the multiplication plots and annual catches obtained from these plots to be more similar compared to other treatments. Further, dissimilarity between catches from control and multiplication plots should be less significant for generations with wet weather conditions during the larval developmental period.

3. If food supply (i.e. the amount of particular qualities of food present in the litter layer **and** accessible to feeding) was the main driving variable, we should expect mass developments in certain taxa on the 5L-plots, at least in years when the multiplied age classes of litter were in a particular state of decay following leaching and initial colonization by microorganisms. Mass developments may be defined as emergence abundance values that are approximately four to five or more times higher than any value recorded from control plots. As it seems resonable to assume that larvae of different species should differ in preferences for particular food qualities, we should also expect to observe a succession of such mass developments in certain species on the 5L-plots whereas, on the exclusion plots, certain taxa and trophic groups should be reduced in numbers due to lack of food thereby causing changes in decomposer community structure.

Obviously, not all of the above hypotheses applies to the responses of all taxa and trophic groups in the dipterous decomposer community. As to the relations of Diptera abundance on different experimental plots, predictions derived from hypothesis 1) and 2) are not contradictory. Most often the sequence 5L > 1L > 0L is found. Judging from abundance curves (fig. 3), macroclimate appears to be the main factor determining the population dynamics of Lauxaniidae [dominant species: [*Lyciella platycephala* (LOEW, 1847)], Fanniidae [*Fannia polychaeta* (STEIN, 1895)], Ceratopogonidae (*Forcipomyia altaica* REMM, 1972), and the sciarid species *Lengersdorfia flabellata* (LENGERSDORF, 1942; fig. 3). As to the similarity of relationships between annual catches from the experimental plots, predictions are but partially fulfilled. In fact, the study period appears to be divided into three parts: 1983, when 5L- and 1L-communities were rather similar, 1984/85, when they were not, and 1986/87, when they were again closely related. (fig. 5, fig. 6A). If macroclimate was the main factor, no close coupling between 5L ('84) and 5L ('85) should have occurred; if moisture was the main factor 1L ('83) and 5L ('83) should have been widely separated. If only phytosaprophagous feeders are considered (fig. 6B), the emerging pattern is in closer accordance with the moisture hypothesis. Nevertheless, phytosaprophagous feeder communities from the multiplication plots were clustered in two groups: one combining the first three study years (1983—85), the other combining the final two years. It is suggested that these findings are due to the third factor: food accessibility.

Mass developments were observed in several species on the multiplication plots (fig. 3): the surface scrapers *Lyciella platycephala* (Lauxaniidae) and *Fannia polychaeta* (Fanniidae) and the phytosaprophagous feeders *Apiloscatopse scutellata* (LOEW, 1846) (Scatopsidae) and *Ep. atomarius* (Sciaridae). Apart from the general influences of macroclimate, the first two species were obviously favoured by the increased supply of food in 1982/83, i.e. multiplied leaf litter which was less than one year old. In *L. platycephala* a peculiar above-ground oviposition behaviour was observed by OEHLERICH (pers. comm.), which should lead to a random distribution of egg batches on the forest floor. In *F. polychaeta*, females are assumed to select oviposition sites suitable for larval development. Thus, the latter species was capable of responding to the still more favourable moisture conditions on the multiplication plots (table 2).

In the phytosaprophagous feeders mass developments were mainly observed in 1984 and 1985. This finding suggests that approximately 1.5- to 2.5-year-old leaf litter is preferred by larval *A. scutellata* and *Ep. atomarius*. It should be borne in mind that rather low C/N-ratios (fig. 2) indicative of high food quality had been recorded when mass developments were observed in these two species. The sciarid genus *Ctenosciara* (almost exclusively *Ct. hyalipennis* (MEIGEN, 1804)), was shown to increase in numbers on both the 5L- and 0L-plots towards the end of the study period. This suggests that larval *Ct. hyalipennis* utilize rather old leaf litter. In the genus *Corynoptera* some indications of successional abundance peaks were observed (fig. 7). Whereas *C. clinochaeta* TUOMIKOSKI, 1960, appears to prefer 1.5-year-old leaf litter, other species seem to be adapted to the utilization of even older age classes of leaf litter: *C. tetrachaeta* TUOMIKOSKI, 1960: 2.5 a; *C. abblanda* FREEMAN, 1983: 2.5—3.5 a; *C. inexpectata* TUOMIKOSKI, 1960: 3.5 a. However, absolute abundance values suggest that the occurrence of *C. clinochaeta* and *C. inexpectata* had been rather favoured by macroclimatic conditions. *C. forcipata* (WINNERTZ, 1867) maintained high abundance values for almost the whole of the study period and larvae appear to be largely favoured by the moist conditions on the 5L-plots.

It is appreciated that the sampling design shows some features of pseudoreplicaton (HURLBERT, 1984). However, it is not likely that variations of physical properties in the mineral soil between experimental plots had been causal to differences in Diptera abundance, as on the multiplication plots the proportion of Diptera larvae extracted from litter layer samples was always much higher than on the control plots (HÖVEMEYER, 1985).

Thus, the overall pattern of succession on the multiplication plots is that surface scrapers and microhumiphagous feeders responded to increased supply of freshly fallen leaf litter, wheras some phytosaprophagous feeders were favoured by the increased amount of partially
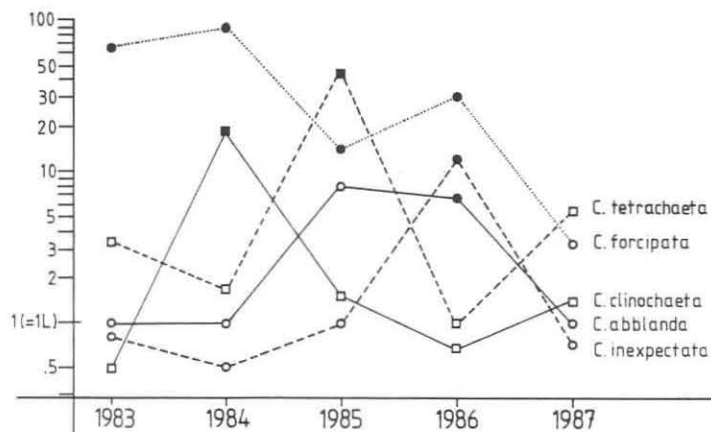
Fig. 7. Relative emergence abundances of five common *Corynoptera* species (Sciaridae) on experimental plots with multiplied canopy leaf litter input (5L) compared to controls (1L) in a beech forest on limestone in five successional years. Factors $< (N_{5L} + 1) (N_{1L} + 1) >$ are given on a logarithmic scale. Full symbols indicate absolute abundance values significantly higher than controls (U-test. $p < 0.05$).

decomposed leaf litter. The succession of abundance peaks in certain species strongly suggests the significance of food supply as an important factor in the limitation of populations in the dipterous decomposer community.

Furthermore. it is not likely that increased moisture content on the 5L-plots should have been the only reason for Diptera numbers ascending to levels approximately 20 to 150 times higher than controls. even if food supply is assumed to have been 10 fold the natural amount. For. if moisture was the main factor determining numbers of Diptera. it remains questionable why it should have acted this way in only one or two out of five years. Thus. it is concluded that food supply was increased by some further mechanism on the 5L-plots. JUDAS (1989) found that on the 5L-plots earthworm biomass was reduced to about 50% the control values. This leaves a lot of unutilized food for Diptera larvae to feed on and we may turn to the discussion of the hypothesis outlined in the introduction.

In moder humus soils earthworm abundance is usually low compared to mull humus soils and Diptera abundance is usually higher. The highest values of adult emergence abundance were reported from moder humus forests and they were due to mass developments of *Ct. hyalipennis* [DORN & JANKE. 1985]. However. the maximum value observed on the multiplication plots during the present study (5L('85)) is, to my knowledge, the third highest ever recorded from any terrestrial ecosystem.

In the litter manipulation experiment no equilibrium conditions were established on the 5L-plots. Therefore. Diptera abundances were not likely to stabilize at some elevated level. Nevertheless. for a short time. the observed responses of Diptera and earthworms to canopy leaf litter multiplication gave rise to a decomposer community, which, if not qualitatively then functionally. exhibited some features typical of moder humus soils. In general. it is suggested that the structural properties of the litter layer may play a significant role in determining the abundance and composition of both the dipterous decomposer community and the decomposer community as a whole.

4. Acknowledgements

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Synopsis: *Original scientific paper*

HÖVEMEYER, K., 1992. Response of Diptera populations to experimentally modified leaf litter input in a beech forest on limestone. Pedobiologia **36**, 35 – 49.

In a submontane beech forest on limestone emergence abundance of adult Diptera was studied on experimental plots with manipulated leaf litter input (1983 – 87). There were four kinds of treatments: **1.** canopy leaf litter input was multiplied in 1981 and 1982 (= 5L); **2.** canopy leaf litter exclusion (1981 – 1987; = OL); **3.** herbaceous leaf litter exclusion (1982 – 84; = OH); **4.** controls. On the 5L-plots annual emergence abundances of total Diptera (maximum: 10 030 ind. m²) and many dipterous families were highest in each study year. On the OL-plots, most families with larvae participating in the decomposition process decreased in numbers except Chironomidae. OL-plots were very similar to controls but Chironomidae increased. In general, population dynamics of many Diptera species and the composition of annual dipterous communities were found to be strongly influenced by macroclimate. Several taxa were obviously favoured by moist conditions on the 5L-plots. A positive effect of increased food supply was observed in several trophic groups (of larvae): microhumiphagous feeders (Chironomidae, Ceratopogonidae) and surface scrapers (Fanniidae, Lauxaniidae) were favoured by an increased supply of fresh beech leaves (1983), whereas mass developments of phytosaprophagous feeders (Scatopsidae, Sciaridae) occurred in two to three-year-old litter (C N-ratio: rd. 26). It is suggested, that structural features of the litter layer may be crucial for determining both the abundance of soil-dwelling Diptera and the composition of the decomposer community.

Keywords: beech forest, Diptera emergence abundance, community structure, leaf litter input, decomposition.

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